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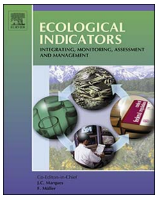

Original Articles

Functional identity of overstorey tree height and understorey conservative traits drive aboveground biomass in a subtropical forest

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ABSTRACT

The niche complementarity hypothesis has received empirical support but species differ in functional strategies for their contribution to ecosystem function, as predicted by the mass ratio hypothesis. Our understanding of how functional identity of conservative and acquisitive strategies of trees predicts aboveground biomass across forest strata (i.e. overstorey and understorey) remains unclear. Aboveground biomass, community-weighted mean (CWM − functional identity) of trait values (6 leaf and 2 stem traits), and soil physicochemical properties were estimated for 125 plots in a 5-ha subtropical forest in Eastern China. We used multiple linear regressions models to relate aboveground biomass to CWM indices at overstorey and understorey strata separately, and whole-community level. We finally employed the structural equation model to test for the effects of overstorey on understorey strata, in addition to the effects of soil physicochemical properties. Forest strata optimal models showed that overstorey strata had high aboveground biomass when they are dominated by functional identity of tree height, whereas high aboveground biomass in understorey strata was driven by functional identity of dense-wooded conservative strategy. Whole-community optimal model showed that communities dominated by functional identity of leaf dry matter content and mean leaf area had high aboveground biomass. Aboveground biomass was negatively related to soil nutrients across forest strata and whole-community level. The structural equation model showed that CWM of overstorey tree height did not affect understorey functional identity and aboveground biomass, when soil physicochemical properties were accounted. Soil nutrients had positive effect on functional identity of overstorey tree height whereas negative effect on functional identity of understorey dense-wooded strategy. This study highlights the fundamental roles of forest strata where overstorey and understorey strata contribute to their corresponding aboveground biomass with contrasting functional strategies across a range of soil nutrients. High aboveground biomass was potentially driven by functional identity of tree height through making use of plentiful soil nutrients at overstorey strata, whereas by conservative strategy at understorey strata through enduring nutrient-poor soils. To better understand the roles of functional identity of conservative and acquisitive strategies in driving ecosystem functions, it is worth to analyse forest strata separately.

1. Introduction

One of the biggest challenges in functional ecology is to explain the underlying mechanisms for the relationships between functional attributes of biodiversity (i.e. functional trait diversity and identity) and ecosystem functions in forest ecosystems. Although the niche complementarity and mass ratio hypotheses have been put forward to explain the relationships between functional attributes of biodiversity and ecosystem functions (e.g. Ali et al., 2017; Conti and D&az, 2013; Finegan et al., 2015; Lin et al., 2016; Prado-Junior et al., 2016), few studies have tested these relationships across forest strata (i.e. overstorey and understorey). The niche complementarity hypothesis based on species richness has received some empirical support across forest strata (e.g. Zhang et al., 2016), but species differ in functional strategies

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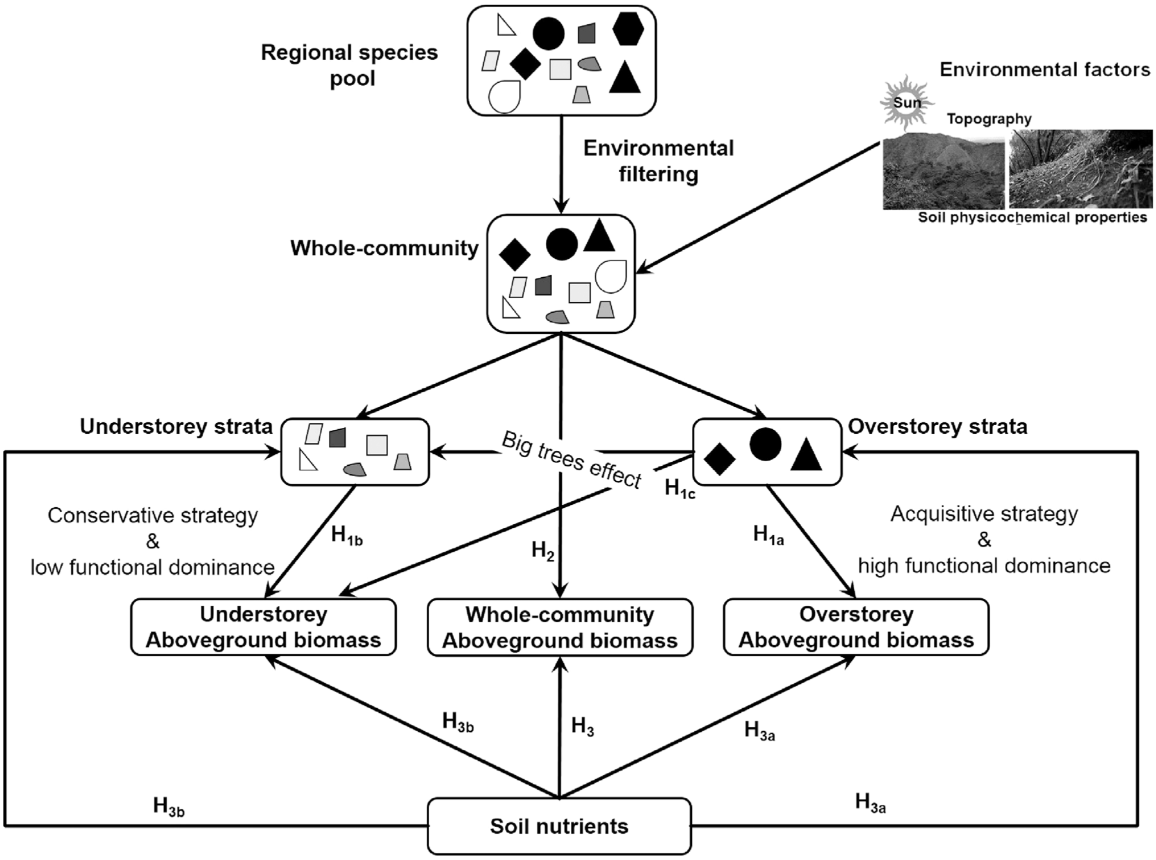

Fig. 1. Conceptual framework showing how changes in aboveground biomass are determined by the mass ratio mechanism. The acquisitive traits were CWM of specific leaf area, mean leaf area, leaf nitrogen and phosphorus concentrations, and ratio of leaf nitrogen to phosphorus concentrations. The conservative traits were CWM of leaf dry matter content and stem wood density. Functional dominance strategy of plant species was represented by CWM of tree maximum height, i.e., functional identity of tree height. Species pool having different symbols represent different species, colors represent different traits such as black color for acquisitive and high functional dominance while white to gray colors for conservative and low functional dominance, and size of the symbols represent the overstorey (big size) and understorey (small size) species. H_{1a}, H_{1b}, H_{1c}, H_2, and H_3 indicate proposed hypotheses, predictions or questions (see introduction section).

for their contribution to ecosystem functions (Rüger et al., 2012) as predicted by the mass ratio hypothesis (Grime, 1998). As such, the relationships between functional attributes of biodiversity and aboveground biomass, especially the associated mechanisms might be fundamentally different across forest strata. To date, few studies have teased apart the contributions of functional attributes of trees with either conservative or acquisitive strategies at overstorey and understorey strata to aboveground biomass in forests.

The mass ratio hypothesis predicts that ecosystem function is driven by the (traits of the) most abundant species in plant communities (Grime, 1998). Aboveground biomass ought to closely relate to community-weighted mean (CWM) of a trait values, i.e., functional identity (Díaz et al., 2007; Garnier et al., 2004; Tobner et al., 2016). With respect to the plant trait syndromes, high CWM of specific leaf area, leaf nitrogen and phosphorus concentrations in plant communities associate with high productivity or aboveground biomass due to fast-growing of acquisitive species (Chiang et al., 2016; Finegan et al., 2015). In contrast, high CWM of leaf dry matter content and wood density indicate a low productivity in communities dominated by conservative species (Garnier et al., 2004; Wright et al., 2010). Additionally, tree species present in overstorey strata are tall stature whereas tree species in understorey strata are short stature. Therefore, tree height and diameter relate to the investment of structure per unit of stem volume, and hence directly influencing its aboveground biomass (Conti and D & az, 2013; Moles et al., 2009). In some extent, the potential maximum plant height or maximum diameter of a given species reflects its adult stature for growth and survival (Poorter and Bongers, 2006; Poorter et al., 2008), and positively relates with productivity or aboveground biomass through functionally dominant strategy (i.e. CWM of plant maximum height or diameter) (Cavanaugh et al., 2014; Finegan et al., 2015; Prado-Junior et al., 2016).

Since light condition is more stressful in understorey than in overstorey in complex natural forests (e.g. Brenes-Arguedas et al., 2011), trees in understorey tend to employ conservative strategy whereas acquisitive strategy may be more apparent in overstorey strata (Bartels and Chen, 2010; Zhang et al., 2016). Previous studies suggest that conservative strategy is crucial for plant species to cope with more stressful environments (i.e., dry forests) (Prado-Junior et al., 2016), whereas acquisitive strategy is advantageous for plant species in more favorable conditions such as in wet and moist forests (Finegan et al., 2015; Malhi et al., 2004). Under the mass ratio hypothesis, high aboveground biomass or productivity is strongly driven by functional identity with either conservative strategy in dry forests (Prado-Junior et al., 2016) or acquisitive strategy in wet and moist forests (Finegan et al., 2015). When the data have been combined across dry and moist tropical forests, Cavanaugh et al. (2014) found that only functional identity matters for high aboveground biomass. Insightfully, these findings provide strong evidence for the presence of big trees effect on available resources for shaping community structure, assemblage and functions. However, as a coin has two sides, big trees in overstorey strata can positively contribute to ecosystem functions through large stem volumes and consumption of resources, but at the same time, they may also slow down the ecosystem functioning rates in understorey strata in forests by reducing light and soil nutrients availabilities (Poorter et al., 2015; Slik et al., 2013; Zhang et al., 2016).

In this study, we tested how aboveground biomass was driven by functional identity with either conservative or acquisitive strategies of tree species at overstorey and understorey strata separately, in addition to the whole-community level in a subtropical forest. Considering the mass ratio effect in overstorey strata where light condition is favorable, we hypothesize (H_{1a}) the positive relationships of aboveground biomass with CWM of acquisitive traits, especially with functional identity of potential maximum tree height, while the negative relationships of aboveground biomass with CWM of conservative traits. With regard to the mass ratio effect in light-stressful understorey, we hypothesize (H_{1b}) the positive relationships of aboveground biomass with CWM of conservative traits, while negative relationships of aboveground biomass with CWM of acquisitive traits. In addition, due to the dominant role of big trees on available resources, we hypothesize (H_{1c}) that functional identity of overstorey strata negatively relates with functional identity and aboveground biomass of understorey strata. For the comparison to whole-community level, we hypothesize (H_2) that high aboveground biomass is potentially driven by high CWM of acquisitive traits due to the dominant role of big trees on the available resources (Fig. 1).

Studies in tropical forests have revealed that soil physicochemical properties should be included when testing multivariate relationships between biodiversity and aboveground biomass because it determines nutrients availability that may strongly influence the relationships between functional traits and aboveground biomass (Chiang et al., 2016; Lin et al., 2016; Prado-Junior et al., 2016). Soil fertility hypothesis predicts that aboveground biomass or productivity increases with increase in soil nutrients availability, and plants can grow faster when resource availability is high (Quesada et al., 2012; Wright et al., 2011). However, high nutrients availability may also lead to increased competition, and hence high mortality and biomass turnover rates of plant species (Prado-Junior et al., 2016). Consequently, high aboveground biomass or productivity in (sub-) tropical forests associates often with nutrient-poor soils (Chiang et al., 2016; Poorter et al., 2015; Prado-Junior et al., 2016). In this case, we hypothesize (H_3) that high CWM of acquisitive trait values relates to nutrient-rich soils (H_{3a}) while high CWM of conservative trait values of understorey associates with nutrient-poor soils (H_{3b}) in driving high aboveground biomass across forest strata.

We tested the above hypotheses by using multiple linear models and structural equation model (SEM) based on the biophysical data from 125 plots inside a 5-ha natural subtropical forest in Eastern China. Specifically, we asked the following two questions: 1) which functional strategy − conservative or acquisitive drives high aboveground biomass across forest strata, while accounting for the effects of soil nutrients? and 2) whether functional identity of overstorey strata affects functional identity and aboveground biomass of understorey strata?

2. Materials and methods

2.1. Study site and forest plots

This study was conducted in a 5-ha subtropical forest plot in Tiantong National forest park (29°48′N, 121°47′E, 200 m a.s.l), located in Ningbo city, Zhejiang province, in Eastern China. The area is characterized by a warm and humid subtropical monsoon climate, with a mean temperature of 28 °C and 4.2 °C in the warmest and coldest months, respectively. The average annual precipitation is 1375 mm, most of which falls between May and August; annual evaporation is 1320 mm and annual relative humidity is 82% (Yan et al., 2013). The vegetation is subtropical evergreen broadleaf forest, and soils are classified as Ferralsols in the FAO soil classification system (World Reference Base for Soil Resources, 2006), with pH values that range from 4.4 to 5.1. The parental material is mostly composed of Mesozoic sediments and intrusive acidic rocks, including quartzite and granite (Ali and Yan, 2017; Yan et al., 2013; Zhang et al., 2012).

The studied 5-ha forest plot is located in the center of the Park, and is divided into 125 20 × 20 m subplots. The topography of the plot is very heterogeneous and rugged (Fig. A.1), with elevation varying from 320.4 to 489.4 m a.s.l. The slopes of the subplots within the plot ranges from 13.8 to 43.9°. The elevation is more pronounced in the northern section than in the southern section of the plot. The western and eastern edges of the plot extended through two north-south oriented valleys, with the interior of the plot spanning two small northwest-to-southeast oriented ridges, approximately 100 m apart (Fig. A.1) (Ali and Yan, 2017).

All stems ≥1 cm DBH were individually tagged, geo-referenced, measured for DBH using a diameter tape and identified to species-level in June to August 2009. A total of 20,253 stems were recorded belonging to 108 species, 76 genera and 43 families. This work was guided on “Observation Methodology for Long-term Forest Ecosystem Research” of National Standards of the People's Republic of China (GB/T 33027-2016). The vertical structure of community and species composition varied with changes in topography. In the ravine area, the canopy tree layer (~15–20 m in height) was dominated by *Choerospondias axiliaris*, which is a deciduous species, whereas the subcanopy tree layer (4 < height < 15 m) was dominated by evergreen species such as *Machilus leptophylla*. The dominant species in the understorey (< 4 m in height) was composed of evergreen species such as *Litsea elongate* and *Eurya loquaiana*. On slopes and ridge areas, the dominant species in understorey was similar to the ravine area. In contrast, the canopy tree layer was occupied by evergreen species including *Lithocarpus harlandii* and *Cyclobalanopsis nubium*, and the subcanopy tree layer was also dominated by evergreen species, such as *Lithocarpus harlandii* (Ali and Yan, 2017).

2.2. Measurement of plant functional traits

We measured eight key functional traits, including two stem traits and six leaf traits, across 98 species in a 5-ha subtropical forest: stem wood density, plant maximum height, specific leaf area, mean leaf area, leaf dry matter content, leaf nitrogen concentration, leaf phosphorous concentration, and leaf nitrogen to phosphorous concentrations ratio. Leaf trait measurements were obtained in the summer (i.e., June to August) of 2010–2013, when trees had fully developed leaves. We measured mean leaf area, specific leaf area and leaf dry matter content for each of the 20,253 individuals in the plots, following Cornelissen et al. (2003). For leaf chemical traits (leaf nitrogen and phosphorous concentrations) and wood density trait measurements were taken for seven randomly-selected healthy mature trees for each species (Cornelissen et al., 2003; Pakeman and Quested, 2007). The trait plant maximum height was collected from the Chinese flora database.

For leaf trait measurements, three branches were cut from three positions (upper, mid, and lower position) in the sunlit side of the tree crown. Twenty to thirty mature leaves (without apparent physical damage) were collected from each branch. The leaves were transported to the laboratory wrapped in a moist paper towel placed in a sealed plastic bag inside a cooler. Functional traits were measured within 12 h after arriving in the laboratory. Twenty leaves were randomly selected from the leaves from each tree, leaf area was determined (using LI-3100C, Li-Cor, USA) and weighted. After that, the leaves were dried at 75 °C for 48 h to determine leaf dry mass. Specific leaf area was calculated as the one-sided area of a leaf divided by its oven-dried mass, mean leaf area as the average leaf area of 20–30 leaves, and leaf dry matter content as the oven-dried mass of a leaf divided by its water-saturated fresh mass (Cornelissen et al., 2003). Finally, the leaf samples collected from an average of seven randomly-selected healthy mature trees were ground to determine leaf nitrogen and phosphorous concentrations using a flow-injection auto analyser (Skalar-1000, Netherland), and then the ratio of leaf nitrogen to phosphorous concentrations (LNC:LPC) was calculated.

For wood density, wood cores were taken on seven individuals for each species with a 5-mm increment corer. In the laboratory, the volume of the tree core was estimated using the length of the tree core, measured using an electronic vernier caliper, and the known diameter. Wood cores were dried at 75 °C in an oven for 72 h to determine dry mass. Wood density was calculated by dividing the dry mass over the volume of the wood sample (Cornelissen et al., 2003).

2.3. Quantification of community-weighted mean of trait values

Overstorey strata were defined as all tree individuals with DBH ≥ 10 cm in each forest plot, and understorey strata included individuals with 1 ≤ DBH < 10 cm (Barrufol et al., 2013). This resulted in a total of 3213 stems belonging to 71 species, 47 genera and 27 families in the overstorey, and a total of 17,004 stems belonging to 94 species, 57 genera and 33 families in the understorey across 125 plots.

For calculation of CWM indices, we used eight functional traits that are important for plant growth and survival (Poorter and Markesteijn, 2008; Wright et al., 2010), and hence for standing aboveground biomass (Finegan et al., 2015; Prado-Junior et al., 2016). We used eight measures of functional identity (8 CWM indices based on a single-trait) that were quantified for the overstorey and understory strata, and whole-community level, separately. The CWM of a single trait (Eq. (1)) was calculated as the mean trait value in the overstorey strata, understorey strata and whole-community level, weighted by the species' relative basal area (Garnier et al., 2004). This metric represents the expected functional trait value of a specific strata or community (Díaz et al., 2007).

$$\mathrm{CWM_x} = \sum_{i=1}^{s} p_i t_i \tag{1}$$

where CWM_x is the CWM for trait x, s is the number of species in the strata or community, p_i is the relative basal area of the ith species in the strata or community and t_i is the trait value for the ith species.

The CWM indices were calculated using the *vegan* (Oksanen et al., 2015), *FD, dbFD* and *functcomp* packages (Laliberté and Legendre, 2010).

2.4. Dataset of soil physicochemical properties

To take into account any effects of soil nutrients and properties on the relationships between functional identity and aboveground biomass, soil carbon content, phosphorus content, nitrogen content, pH, volumetric soil water content, bulk density and humus depth were included in the statistical analyses. The original dataset of soil physicochemical properties for each sampling plot within a 5-ha forest plot were used from the study of Zhang et al. (2012). In order to reduce the number of local soil properties and to avoid the strong correlations among them (see Supplementary Material in Table A.1 for correlations), we ran a principal component analyses (PCA) based on the soil physicochemical properties. The first multivariate axis of PCA (PC 1, 49%) was mostly defined by soil physicochemical properties including soil carbon content, pH, volumetric soil water content, bulk density and humus depth, whereas soil phosphorus content had fair contribution but soil nitrogen content had relatively less contribution. The second multivariate axis of PCA (PC2, 27%) was mostly defined by soil nutrients including soil phosphorus and nitrogen contents in addition to the fair contribution of soil physicochemical properties. In all statistical analyses, we used two PCA axes for soil physicochemical properties (see Table A.2).

2.5. Estimation of aboveground biomass

We calculated aboveground biomass for each tree with DBH ≥ 5 cm (AGB*t*) using a global allometric equation (Eq. (2)) (Chave et al., 2014), which is based on tree DBH, site-specific environment stress factor (E) and species' wood density (ρ).

$$\mathrm{AGB}t = \exp\{-1.803 - 0.976(\mathrm{E}) + 0.976 \times \ln(\rho) + 2.673 \times \ln(\mathrm{DBH}) - 0.0299 \times (\ln(\mathrm{DBH}))^2 \tag{2}$$

Where E for our study site was derived from (Chave et al., 2014).

We estimated aboveground biomass of shrubs and small trees (AGB*s*) with DBH < 5 cm using a general multi-species allometric equation (Eq. (3)) developed locally for small trees (Ali et al., 2015), which is similarly based on tree DBH and species' wood density (ρ).

$$\mathrm{AGB}s = 1.450 \times \exp\{-4.97 + 2.20 \times \ln(\mathrm{DBH}) + 3.06(\rho)\} \tag{3}$$

Finally, we quantified aboveground biomass for overstorey and understorey strata through the summation of aboveground biomass of trees having DBH ≥ 10 cm and 1 ≤ DBH < 10 cm, respectively. The aboveground biomass of overstorey and understorey strata within each plot was converted to megagram per hectare ($\mathrm{Mg\ ha^{-1}}$).

2.6. Statistical analyses

Our study design may confound statistical results when there is spatial autocorrelation in the variables of interest. To account for this we performed generalized least-squares (GLS) models (Pinheiro and Bates, 2016), with (accounted for the spatial location of each subplot, i.e. local X and Y coordinates within a 5-ha plot) and without spatial autocorrelation among subplots for each of the relationships between predictors and aboveground biomass, as recommended by previous studies (Chisholm et al., 2013; Yuan et al., 2016). In addition, forest strata may also confound the spatial autocorrelation in the variables of interest, as overstorey and understorey strata within a plot have similar spatial location (X and Y coordinates). We therefore explicitly accounted for the effect of forest strata (overstorey and understorey), using grouping variable, on the relationship between predictor and aboveground biomass in both spatial and non-spatial GLS models. GLS model is a reliable method for testing whether subplots sharing the same abiotic conditions are independent from each other within a forest (Zuur et al., 2009). The goodness of fit of spatial and non-spatial GLS models was evaluated by AIC, and we found that models without spatial autocorrelation always had the lower AIC values (Tables A.3 and A.4), which is similar to the recent observations in 25-ha broad-leaved Korean pine mixed forest and 5-ha secondary poplar-birch forest in northeastern China (Yuan et al., 2016).

Having found no strong evidences for spatial autocorrelation, we then performed multiple linear regressions models (i.e., general linear models) to evaluate how aboveground biomass related to CWM of trait values at each of overstorey and understorey strata across a range of local soil conditions (see conceptual framework in Fig. 1). More specifically, we included all CWM of trait values (8 indices) in order to test for the joint effects of the functional identity of conservative and acquisitive strategies of studied trees on aboveground biomass at each of the overstorey and understorey strata, and whole-community level. In all models, we included local soil factors, i.e., soil PC1 and soil PC2, as covariates. We used all subsets regression analysis and selected the optimal model that had lowest AICc (i.e. AIC adjusted for small sample sizes). Models were considered to be equally supported if the difference in AICc was less than two units (Bartoń, 2016). When models were equally supported, we selected the most parsimonious model by considering the lowest number of predictors. General linear models were performed using the *stats* package and all subsets regression analyses using the *MuMIn* package (Bartoń, 2016). We plotted a bivariate model's response (optimal linear model) against each predictor's marginal effect (i.e. holding all other predictors in constant), by using the *plotmo* package (Milborrow, 2015). In addition, we applied the Moran's I test for spatial autocorrelation in the selected optimal linear model residuals, while assessing the range and type of spatial autocorrelation in lag classes by plotting the correlograms (Fig. A.2), by using the *spdep* package (Bivand, 2016). The complementary Pearson's correlations between all tested predictors at each of the overstorey and understorey strata, and whole-community level are shown in Tables A.5, A.6 and A.7, respectively.

Finally, we employed SEM in order to evaluate whether CWM of trait values of overstorey strata affect CWM of trait values of at understorey strata and its relationship with aboveground biomass, by simultaneously accounting for the effects of soil nutrients and physicochemical properties. Here, we selected the best predictors for aboveground biomass which were retained in the selected optimal model for overstorey and understorey strata. In order to keep possible consistency with the optimal linear model and to answer our question, we constructed SEM based on the following three paths: 1) direct effects of overstorey CWM of trait values on understorey's CWM of trait values and aboveground biomass, after accounting for the effects of soil factors (PC1 and PC2); 2) indirect effects of overstorey CWM of trait values on understorey aboveground biomass via understorey CWM of trait values; and 3) direct effects of soil factors and understorey CWM of trait values on understorey aboveground biomass. Best-fit SEM was assessed through several tests (Malaeb et al., 2000), including the Chi-square (χ^2) test, goodness-of-fit index (GFI), comparative fit index (CFI) and standardized root mean square residual (SRMR). The SEM was implemented using the *lavaan* package (Rosseel, 2012).

Prior to the statistical analyses, Shapiro-Wilk goodness-of-fit test was used to assess the normality for all variables. All numerical variables including aboveground biomass and CWM of trait values were natural-logarithm transformed and standardized. Transformations of the variables were conducted for the purpose to meet the assumptions of normality and linearity, and to reduce the effect of outliers and to account for possible nonlinear relationships between variables, and to allow comparisons among multiple predictors and models (Zuur et al., 2009). The dataset used in the analyses is provided in Appendix B. For all statistical analyses R 3.2.2 was used (R Development Core and Team, 2015).

3. Results

3.1. Bivariate relationships between aboveground biomass and each of CWM of trait values and soil properties

Bivariate relationships showed that, in overstorey strata, aboveground biomass significantly increased with increasing CWM of tree height (i.e. functional identity of tree height) only (Fig. 2). In understorey strata, aboveground biomass significantly increased with increasing CWM of leaf dry matter content and stem wood density, but significantly decreased with increasing CWM of mean leaf area, specific leaf area, leaf nitrogen concentration and LNC:LPC, as well as with increasing CWM of tree height (Fig. 3). At the whole-community level, aboveground biomass significantly increased with increasing CWM of tree height and leaf dry matter content (Fig. 4). The CWM of other trait values did not significantly relate to aboveground biomass in overstorey and understorey strata, and whole-community level (Table A.8). In addition, aboveground biomass in overstorey and understorey strata, as well as in whole-community level was consistently negative related to soil nutrients (PC2 axis), while soil physiochemical properties (PC1 axis) only negatively related to aboveground biomass of understorey strata (Figs. 2, 3 and 4).

3.2. Effects of functional identity of conservative and acquisitive strategies on aboveground biomass

The overstorey strata optimal model showed that aboveground biomass of overstorey strata was best predicted ($R^2 = 0.20$) by CWM of tree height ($\beta = 0.41$, $P < 0.001$) and soil nutrients ($\beta = -0.22$, $P < 0.001$) (Table 1; Fig. 5A). The understorey strata optimal model showed that aboveground biomass of understorey strata was best predicted ($R^2 = 0.44$) by CWM of stem wood density ($\beta = 0.22$, $P = 0.032$), soil nutrients ($\beta = -0.33$, $P < 0.001$) and physicochemical properties ($\beta = -0.10$, $P = 0.023$) (Table 1; Fig. 5B). In comparison, the whole-community optimal model showed that aboveground biomass was best predicted ($R^2 = 0.32$) by CWM of tree height ($\beta = 0.48$, $P < 0.001$), leaf dry matter content ($\beta = 0.24$, $P = 0.014$), mean leaf area ($\beta = 0.27$, $P = 0.013$) and soil nutrients ($\beta = -0.31$, $P < 0.001$) (Table 1; Fig. 5C).

3.3. The big trees effect on functional identity and aboveground biomass in understorey

The best-fit SEM (Fig. 6) showed that CWM of overstorey tree height did not directly affect both CWM of stem wood density ($\beta = -0.04$, $P = 0.549$) and aboveground biomass ($\beta = -0.07$, $P = 0.286$) of understorey strata. Also, CWM of overstorey tree height had the non-significant negative indirect effect on understorey aboveground biomass via CWM of stem wood density of understorey, and hence the total (direct + indirect effects) negative effect was not significant (Table 2). Interestingly, soil nutrients had the direct positive effect on CWM of overstorey tree height ($\beta = 0.21$, $P = 0.017$). In contrast, soil nutrients and physicochemical properties had direct negative effects on the CWM of stem wood density (β = –0.55 and -0.49, $P < 0.001$) and aboveground biomass ($\beta = -0.44$ and -0.20, $P < 0.001$ and 0.013; Fig. 6) in understorey strata. Soil nutrients had indirect negative effects on understorey aboveground biomass via CWM of understorey's stem wood density but non-significant via CWM of overstorey tree height. The total effect of soil nutrients on understorey aboveground biomass was significantly negative (β = –0.57, $P < 0.001$; Table 2).

4. Discussion

In partial agreement with our specific hypothesis (H_1), we found that high aboveground biomass is potentially driven by functional identity of tall trees in overstorey strata, whereas by dense-wooded conservative trees in understorey strata, respectively. In comparison, high aboveground biomass is associated with high CWM of tree height, leaf dry matter content and mean leaf area at whole-community level. These results provide strong evidence to the functional strategy-dependent mass ratio mechanisms driving aboveground biomass across forest strata within a subtropical forest. This study highlights the fundamental roles of forest strata where overstorey and understorey strata contribute to their corresponding aboveground biomass with contrasting strategies based on functional identity across a range of local soil nutrients and physicochemical properties.

4.1. Functional identity of tree height drives high aboveground biomass in overstorey strata

It is plausible that tall and big trees with positive allometric relationship between height and diameter have large stem volumes, thus substantially contributing to the aboveground biomass (Chave et al., 2009), due to the big trees effect on the available resources (e.g. Slik et al., 2013). This result agrees with previous studies that the relative abundance, stand basal area and functional identity of tall and big trees have a large effect on aboveground biomass (Balvanera et al., 2005; Cavanaugh et al., 2014; Lohbeck et al., 2016; Slik et al., 2013) and productivity (Prado-Junior et al., 2016). Our result as well as those from previous studies, collectively support the selection effect hypothesis or the mass ratio hypothesis, which highlights the importance of dominant species in maintaining ecosystem function (Cardinale et al., 2012; Loreau and Hector, 2001).

Interestingly, the CWM of wood density and leaf traits appeared to be unimportant for driving aboveground biomass at the overstorey strata, and hence no any clear or significant evidence for the effects of the conservative or acquisitive strategy of trees on aboveground biomass in overstorey strata. This result suggests that the functional identity of tree height, and to a lesser extent wood density and leaf

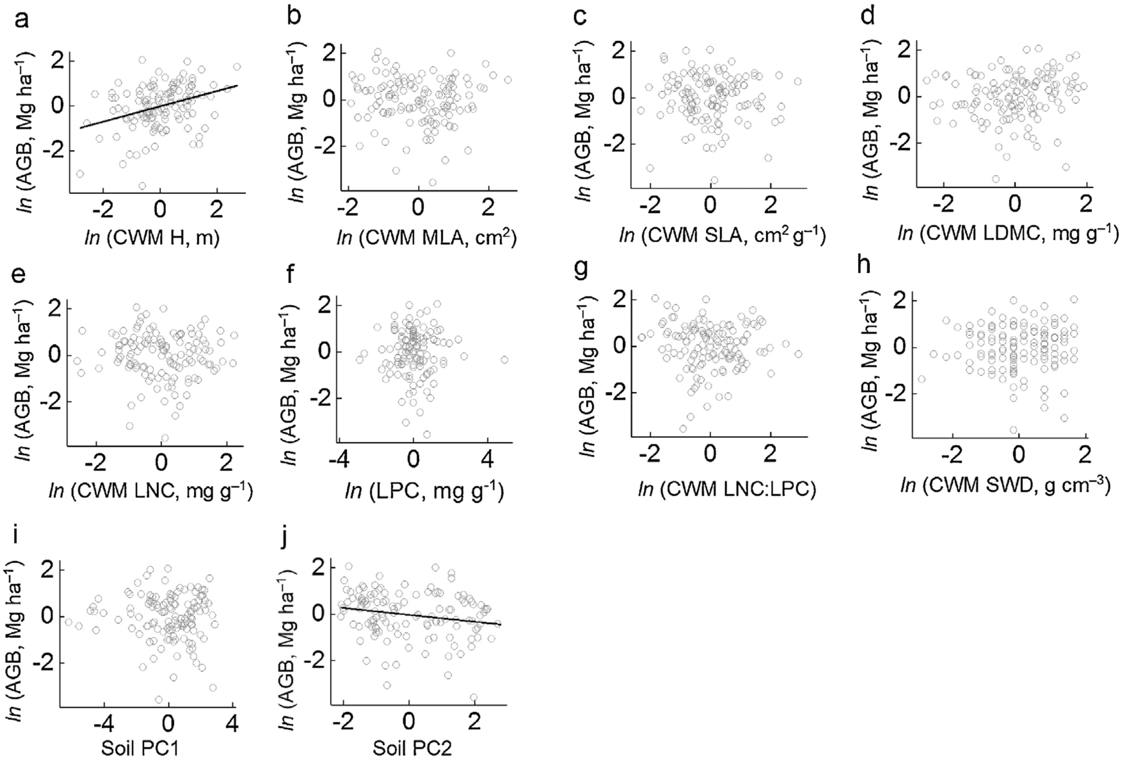

Fig. 2. The bivariate relationships between aboveground biomass (AGB) and predictors (a-h, CWM of trait values; and i-j, soil physiochemical properties axes; $n = 125$) at overstorey strata in a subtropical evergreen broadleaf forest in Eastern China. Fitted regressions are significant at $P < 0.05$. Abbreviations: CWM, community-weighted mean; H, plant maximum potential height; SLA, specific leaf area; LDMC, leaf dry matter content; MLA, mean leaf area; LNC, leaf nitrogen concentration; LPC, leaf phosphorus concentration; LNC:LPC leaf nitrogen to phosphorus ratio; SWD, stem wood density; PC1 and PC2, PCA axes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

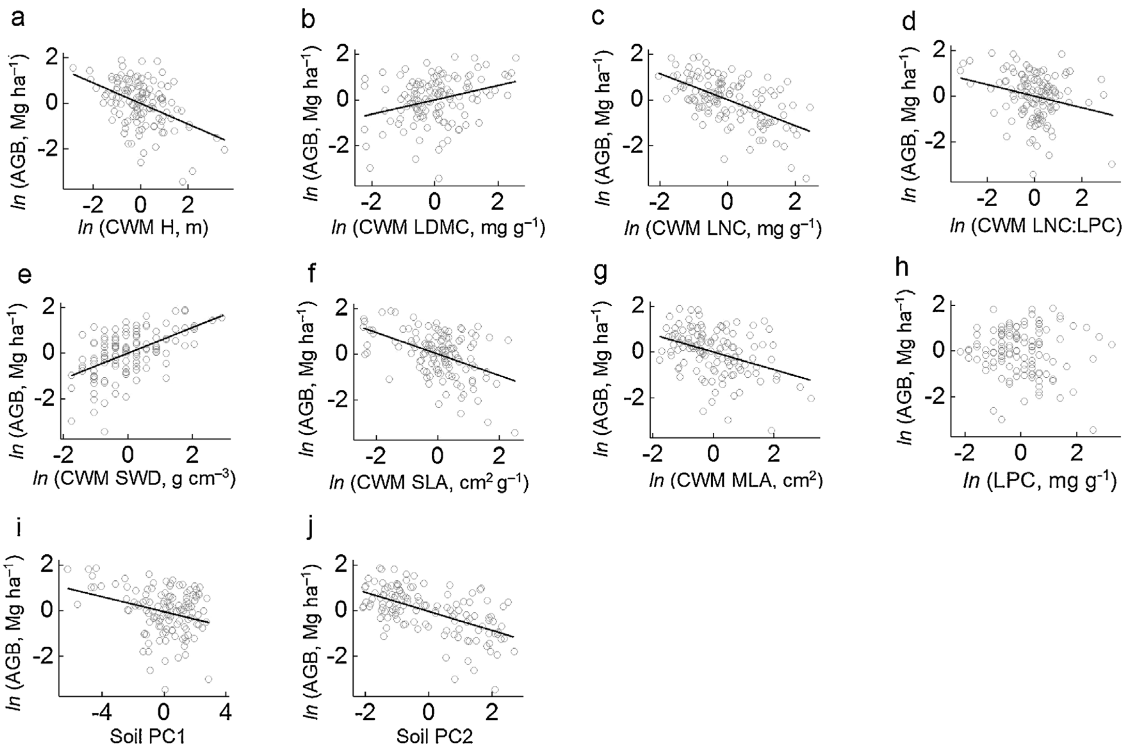

Fig. 3. The bivariate relationships between aboveground biomass (AGB) and predictors (a-h, CWM of trait values; and i-j, soil physiochemical properties axes; $n = 125$) at understorey strata in a subtropical evergreen broadleaf forest in Eastern China. Fitted regressions are significant at $P < 0.05$. All the abbreviations for variables are explained in Fig. 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

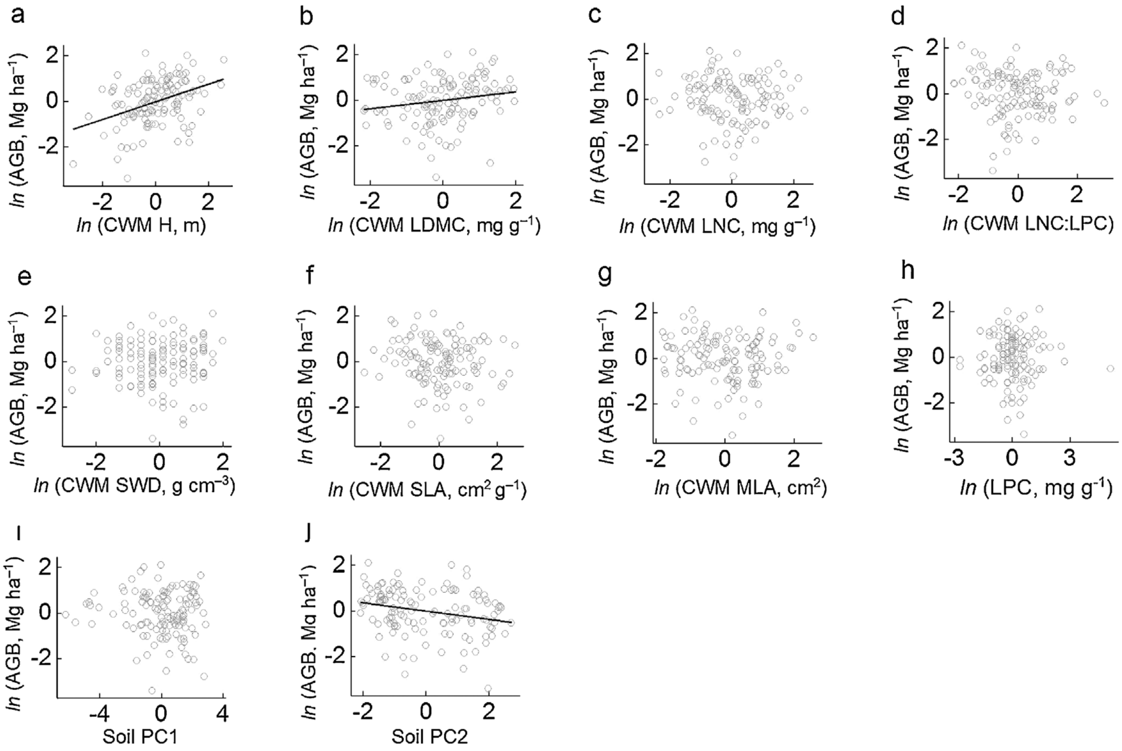

Fig. 4. The bivariate relationships between aboveground biomass (AGB) and predictors (a-h, CWM of trait values; and i-j, soil physiochemical properties axes; $n = 125$) at whole-community level in a subtropical evergreen broadleaf forest in Eastern China. Fitted regressions are significant at $P < 0.05$. All the abbreviations for variables are explained in Fig. 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

traits, with a narrow range of functional trait variation best explain aboveground biomass in natural forests (Conti and Díaz, 2013). However, our result and those of previous studies (Cavanaugh et al., 2014; Conti and D & az, 2013) argue against the general hypotheses that aboveground biomass is related to the high stature trees with either dense-wooded or light-wooded species (e.g. Stegen et al., 2009), and either with nutrient-rich and nutrient-poor leaves species (Finegan et al., 2015; Prado-Junior et al., 2016). Our results suggest that an increase of the functional identity of tree height of overstorey trees, rather than conservative or acquisitive strategy, may enhance aboveground biomass or productivity (Cavanaugh et al., 2014; Conti and D & az, 2013), probably due to their better response to environmental filtering (Lasky et al., 2014; Zhang et al., 2016). Our study was local in its spatial extent, and therefore our results indicate that the positive relationship between functional identity of tree height and aboveground biomass is consistent across a variety of scales, i.e. local,

Table 1

The overstorey strata, understorey strata and whole-community level optimal models obtained from a series of multiple regression analyses for aboveground biomass and 10 predictors (8 CWM indices, and 2 soil PCA axes within each model) using linear model. Standardized regression coefficient (Beta), *t*-test and *P*-value are given. The coefficient of determination (R^2), *F*-test, *P*-value and Akaike Information Criterion (AICc) of the model are also given. *P* values < 0.05 are given in bold. Moran's *I* test was conducted on the residuals for optimal linear model ($P > 0.05$ indicates no spatial autocorrelation). The blank cells represent that predictor variables were not retained in the selected optimal model. Model selection table is shown in Table A.9. All the abbreviations for variables are explained in Fig. 2.

Predictors	Overstorey strata model			Understorey strata model			Whole-community model		
	Beta	*t*	*P*	Beta	*t*	*P*	Beta	*t*	*P*
Constant	0.00	0.00	0.998	0.00	−0.01	0.992	0.00	0.00	0.999
Mass ratio hypothesis (community-weighted mean of a trait)									
CWM H	0.41	4.92	**< 0.001**				0.48	6.15	**< 0.001**
CWM SLA									
CWM LDMC							0.24	2.49	**0.014**
CWM MLA							0.27	2.52	**0.013**
CWM LNC									
CWM LPC									
CWM LNC:LPC									
CWM SWD				0.22	2.17	**0.032**			
Soil physicochemical properties axes									
Soil PC1				−0.10	−2.31	**0.023**			
Soil PC2	−0.22	−3.59	**< 0.001**	−0.33	−5.16	**< 0.001**	−0.31	−4.72	**< 0.001**
Model statistics									
F-test (*P*-value)	15.52 (**< 0.001**)			32.13 (**< 0.001**)			14.75 (**< 0.001**)		
R^2	0.20			0.44			0.32		
AICc	333.5			291.2			316.4		
Moran's *I*- test (*P*-value)	−0.003 (0.917)			0.05 (0.225)			0.02 (0.608)		

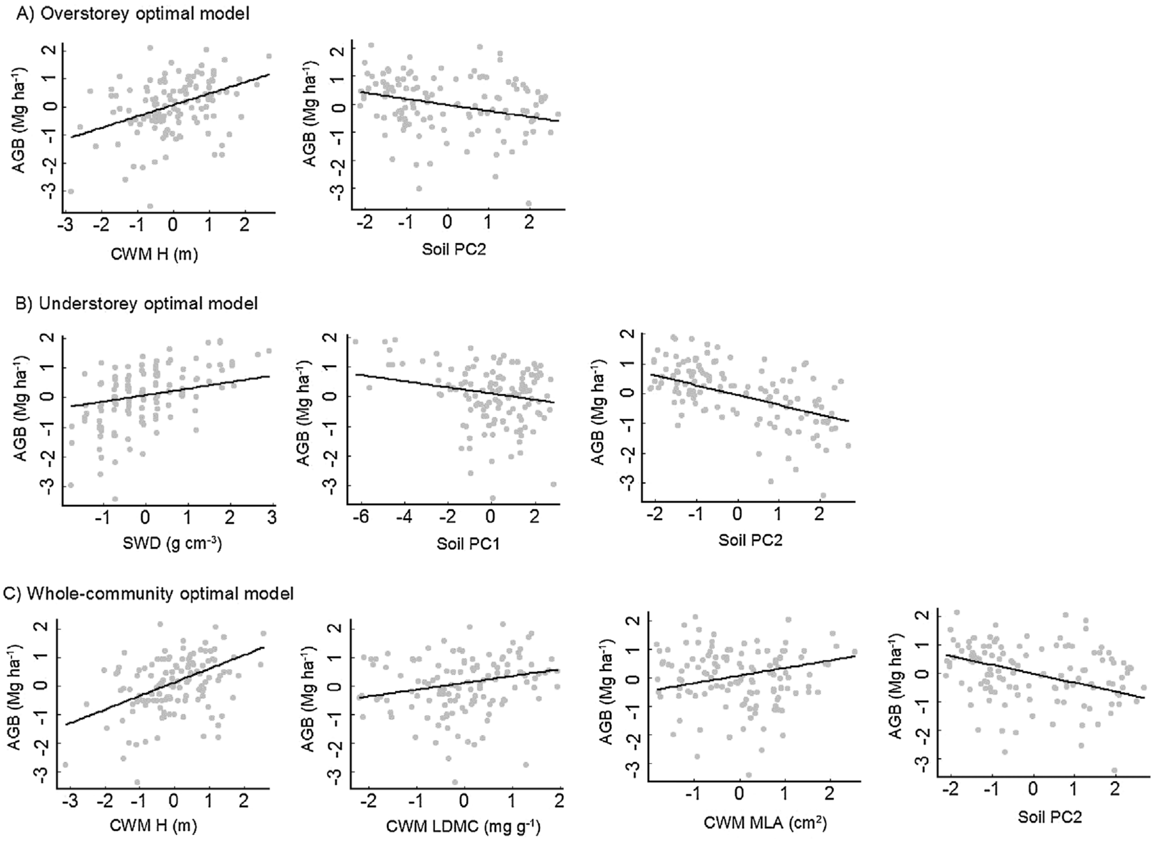

Fig. 5. The response of aboveground biomass to the retained predictors in the overstorey strata (A), understorey strata (B) and whole-community level (C) optimal models (see Table 1 for statistics). The partial dependence plots represent an optimal linear model's response when varying predictor while holding the other predictors constant (i.e. marginal effect of a predictor). Solid lines represent significant ($P < 0.05$) relationships. See Figs. 2, 3 and 4 for bivariate relationships. All the abbreviations for variables are explained in Fig. 2.

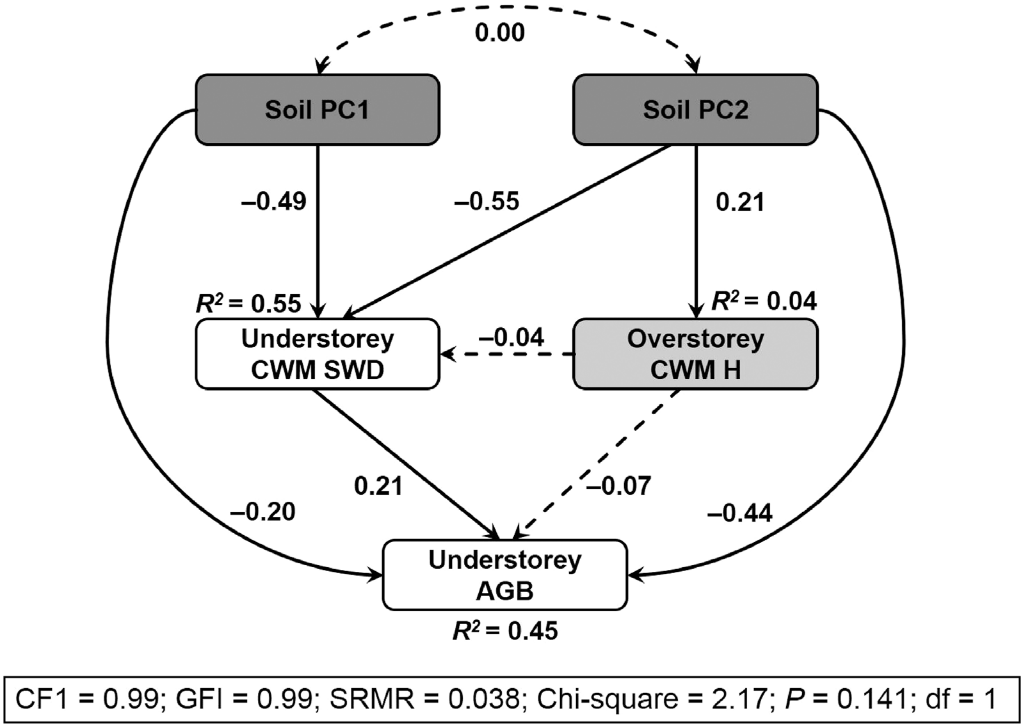

Fig. 6. Best-fit structural equation model (SEM) linking functional identity of overstorey (i.e. CWM H) and understorey strata (i.e. CWM SWD), and soil physicochemical properties (i.e. soil PC1 and PC2) with understorey aboveground biomass. Solid arrows represent significant ($P < 0.05$) paths and dashed arrows represent non-significant paths ($P > 0.05$). For each path the standardized regression coefficient is shown. R^2 indicates the total variation in a dependent variable that is explained by the combined independent variables. Model-fit statistics are provided. The variables in SEM were selected based on selected optimal models for overstorey and understorey strata obtained from a series of multiple regressions (see Table 1). Abbreviations: AGB, aboveground biomass; CWM H, community-weighted mean of tree height; CWM SWD, community-weighted mean of stem wood density; CFI, comparative fit index; GFI, goodness of fit index; SRMR, standardized root mean square residual; df, degree of freedom.

Table 2
The direct, indirect, and total standardized effects of soil nutrients, overstorey and understorey functional identity (i.e. CWM of a trait values) on understorey aboveground biomass based on structural equation model (SEM). Significant effects are indicated in bold ($P < 0.05$). All the abbreviations for variables are explained in Fig. 2.

Predictor	Pathway to understorey aboveground biomass	Model in Fig. 6	
		Effect	*P*-value
Soil properties (PC1)	Direct effect	−0.20	0.013
	Indirect effect via understorey CWM SWD	−0.10	0.037
	Total effect	−0.31	**< 0.001**
Soil nutrients (PC2)	Direct effect	−0.44	**< 0.001**
	Indirect effect via overstorey CWM H	−0.02	0.330
	Indirect effect via understorey CWM SWD	−0.12	**0.036**
	Total effect	−0.57	**< 0.001**
Overstorey CWM H	Direct effect	−0.07	0.286
	Indirect effect via understorey CWM SWD	−0.01	0.563
	Total effect	−0.08	0.245
Understorey CWM SWD	Direct effect	0.21	**0.031**

regional, continent and global scales (Baker et al., 2009; Cavanaugh et al., 2014; Conti and D & az, 2013; Slik et al., 2013).

4.2. *Conservative strategy drives high aboveground biomass in understorey strata*

Surprisingly, as hypothesized we found that understorey strata dominated by slow-growing conservative species (i.e. low leaf nitrogen and phosphorus concentrations, low specific leaf area, and high wood density and leaf dry matter content) had high aboveground biomass (Table 1; Fig. 3). Our results suggest that slow-growing conservative species driving high aboveground biomass in the resource-limited environments (e.g. understorey strata in our study) (Chave et al., 2009; Prado-Junior et al., 2016). We found that functional identity of tree height was not the most important variable for aboveground biomass in understorey strata. The negative bivariate relationship between CWM of tree height and aboveground biomass might relate to the various underlying demographic processes in understorey strata (Poorter and Markesteijn, 2008; Russo et al., 2008). Further research is needed to disentangle how different drivers affect different demographic processes, and hence net aboveground biomass change (Prado-Junior et al., 2016). However, this negative relationship might happen due to the slow growth of understorey species, as a result of the strong light limitation in understorey strata (Rüger et al., 2012).

Our study showed that the acquisitive-conservative trait spectrum has different consequences for overstorey and understorey strata. The major resources needed for plant growth and survival are light, water and nutrients (Jucker et al., 2014; Sterck et al., 2011). It has been hypothesized that the niche complementarity effect may be less important in stable and productive environments, where competition is often the most common form of species interaction, than in unstable and stressful environments (Paquette and Messier, 2011). Our findings confirm that resource-use complementarity of the conservative strategy of the species manifests under resource-limiting environments (Prado-Junior et al., 2016; Sterck et al., 2011) − in our case the understorey strata of a subtropical forest.

4.3. *The big trees effect on understorey functional identity and aboveground biomass*

Overstorey strata with great tree size consume a plenty of resources such as light and water, thus remaining few resources to the trees in understorey strata (Bartels and Chen, 2010, 2013). The dominant filtering role of overstorey strata on the available resources may therefore impose negative influence on the aboveground biomass in understorey strata probably due to the limited resources availability (Bartels and Chen, 2013; Hooper et al., 2005; Zhang et al., 2016). This pattern can be clearly evidenced by the positive effect of soil nutrients on CWM of overstorey tree height and the negative effect of soil nutrients on CWM of understorey stem wood density (Fig. 6). Water and nutrients are more plentiful for trees in overstorey strata because they have large root systems that efficiently absorb these resources. Hence, the positive response of overstorey functional identity of tree height to soil nutrients has probably indirectly reduced resources in understorey strata. However, the big trees effect does not work directly on functional identity and aboveground biomass of understorey strata in this study (Fig. 6). This might happen due to the resource heterogeneity in understorey strata caused by overstorey stand structure, which in turn affects species diversity and thus functional identity of understorey (Bartels and Chen, 2013; Zhang et al., 2016).

In comparison, the whole-community optimal model showed that high aboveground biomass is strongly driven by functional identity of tall and big trees with high leaf dry matter content (conservative strategy) and mean leaf area (acquisitive strategy). This result may be attributable to the selection effect, i.e., diverse communities are more likely to by chance include certain productive, high-functioning species and traits (Loreau and Hector, 2001), and hence high aboveground biomass (Cavanaugh et al., 2014).

4.4. *Soil nutrients modulate functional strategies for driving high aboveground biomass across forest strata*

In contrary to the soil fertility hypothesis, we found that soil nutrients had negative effect on aboveground biomass at each of overstorey and understorey strata, and whole-community level. These negative relationships may be attributable to species adaptations to the local soil conditions through increasing longevity and stand biomass retention (Jucker et al., 2016; Poorter et al., 2015; Prado-Junior et al., 2016). Besides the direct effects, soil nutrients can also indirectly affect aboveground biomass via edaphic filtering (Jucker et al., 2016; Reich, 2014). Nutrient-poor soils tend to be dominated by species with conservative strategy, whereas nutrient-rich soils tend to be dominated by species with acquisitive strategy (Fortunel et al., 2014; Poorter and Bongers, 2006; Reich, 2014).

As expected, we found that, on the one hand, soil nutrients positively affect functional identity of tree height in overstorey strata but negatively affect the overstorey aboveground biomass, indicating a fast-growing strategy for overstorey trees. On the other hand, strong negative direct effects of soil nutrients and physicochemical on understorey functional identity and aboveground biomass indicate a slow-growing conservative strategy for nutrient-tolerant trees in understorey strata. It is plausible that trees with conservative trait values (e.g. high wood density) dominate on nutrient-poor soils because dense-wooded trees enhance nutrient residence time in the trees (e.g. Prado-Junior et al., 2016). In our studied forest, the same conservative trait values are important to deal with nutrient-limited environment (i.e. understorey strata), and hence enhances aboveground biomass through conservative strategy. In addition, our results showed that direct effect of overstorey functional identity of tree height had no significant effects on the understorey's functional identity and aboveground biomass. In combination, our study suggests that in understorey strata of the forest, soil nutrients (i.e. the big trees effect on the available resources) may be a stronger driver of aboveground biomass than light availability in a subtropical forest.

5. Concluding remarks

We conclude that the roles of functional identity of conservative and acquisitive strategies based on the mass ratio hypothesis for predicting aboveground biomass depend on the individual strata of concern. The big trees effect on the available resources has probably caused reduction in resources in the understorey strata, and hence trees in understorey tended to employ conservative strategy for driving high aboveground biomass. High aboveground biomass was potentially driven by tall stature or functional identity of tree height through making use of plentiful soil nutrients at overstorey strata, whereas by conservative strategy at understorey strata through enduring nutrient-poor soils, simultaneously both strategies do so at the whole-community level. Our study suggests that in complex subtropical forest, combining data across forest strata may swamp the contrasting observed relationships at overstorey and understorey strata. Therefore, to better understand the roles of functional identity of conservative and acquisitive strategies in driving ecosystem functions, it is worth to analyse the overstorey and understorey strata separately.

Data availability

Dataset used for analyses accompanies this paper as supplementary file (Appendix B). More information about dataset are available upon request to the authors.

Conflict of interest

The authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2017.07.054.

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